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Complex courtship displays facilitate male reproductive success and plasticity in signaling across variable environments

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Complex courtship displays facilitate male reproductive success and plasticity in signaling across variable environments

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Abstract Effective signal transmission is essential for communication. In environments where signal transmission is highly variable, signalers may utilize complex signals, which incorporate multiple components and modalities, to maintain effective communication. Male *Rabidosa rabida* wolf spiders produce complex courtship signals, consisting of both visual and seismic components. We test the hypothesis that the complex signaling of *R. rabida* contributes to male reproductive success in variable signaling environments. We first examine the condition-dependence of foreleg ornamentation (a presumed visual signal) and seismic signal components and find that both may provide potentially redundant information on foraging history. Next, we assessed reproductive success across manipulated signaling environments that varied in the effectiveness of visual and/or seismic signal transmission. In environments where only one signal could be successfully transmitted (e.g., visual or seismic), pairs were still able to successfully copulate. Additionally, we found that males altered their courtship display depending on the current signaling environment. Specifically, males reduced their use of a visual display component in signaling environments where visual signal transmission was ablated. Incorporating signals in multiple modalities not only enables *R. rabida* males to maintain copulation success across variable signaling environments, but it also enables males to adjust their composite courtship display to current signaling conditions [*Current Zoology* 57 (2): 175–186, 2011].

Keywords Communication, Multimodal, Signal evolution, Condition-dependent, Lycosidae, *Rabidosa rabida*, Efficacy back-up, Redundant signals

The environment is an important source of selection on both signalers and receivers and has had a considerable influence on the evolution of reproductive communication (Endler, 1992; 1993; Boughman, 2002). While the messages conveyed in signals are often important in influencing receiver decisions, in order to be effective, these messages must transmit through the environment and remain recognizable to the receiver (Guilford and Dawkins, 1991). Across taxa and encompassing multiple signaling modalities, the environment has been suggested to shape male mating signals for maximizing detection and discrimination by receiving females (e.g., Ryan and Wilczynski, 1991; Boughman, 2001; Elias et al., 2004; Leal and Fleishman, 2004; Cokl et al., 2005; Cocroft et al., 2006; Seehausen et al., 2008; Elias et al., 2010). While this signal-environment match benefits males in homogenous environments, many males regularly encounter variable environments. Often, this variability favors selective signaling behavior, where male courtship displays tend to occur in environments that maximize signaling efficacy (e.g., Endler, 1991; Endler and Thery, 1996; Andersson et al., 1998; Kotiaho et al., 2000; Heindl and Winkler, 2003; McNett and Cocroft, 2008). While selective signaling may be favored by reducing unnecessary costs when signals are unlikely to be recognizable, it also limits potential reproductive activity and associated benefits, which could have important fitness consequences. Thus, for males encountering multiple signaling environments, selection may favor male displays that transmit information effectively in multiple environments (Hebets et al., 2008a).

Males faced with variable environments could use a generalized signal that would transmit (often sub-optimally) across several environments (e.g. Hebets et al., 2008a; Milner et al., 2008). Use of such a generalized signal might lead to some males modifying signals behaviorally (e.g., amplitude, duration, velocity) to increase detection probabilities (e.g., Patricelli and Blickley, 2006; Ord et al., 2007; Peters et al., 2007). Alternatively, males could use displays that incorporate

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multiple signals or related components across different sensory modalities (i.e., complex displays). In this scenario, selection from different sources (i.e., environments) could act separately on various signal components to optimize the efficacy of information transfer across a multitude of signaling environments (reviewed in Candolin, 2003; Hebets and Papaj, 2005). When detection across variable environments is an issue, selection may act on signal form to enhance transmission, while maintaining similar information content. Thus, selection may lead to the evolution of complex signaling incorporating redundant information across signal components, (Møller and Pomiankowski, 1993; Johnstone, 1995), enabling both accurate and consistent female assessment regardless of the environment (Candolin, 2003; Partan and Marler, 2005).

Complex displays are common across the animal kingdom and numerous hypotheses exist regarding their function (see reviews in Partan and Marler, 1999; Rowe, 1999; Candolin, 2003; Hebets and Papaj, 2005; Partan and Marler, 2005). Recent empirical as well as theoretical work highlights the role of variable and dynamic environments in the evolution of signal complexity (e.g., Candolin, 2003; Peters and Evans, 2003; Ord and Martins, 2006; Peters et al., 2008; Bro-Jørgensen, 2009; Heuschele et al., 2009). Work on spiders has provided considerable insight into the evolution of multimodal signals used in mate choice (Coleman, 2009). In particular, wolf spiders (Araneae: Lycosidae) are known for their incredible diversity and complexity of male courtship displays. Male courtship varies in the number of modalities incorporated into displays (e.g. seismic, visual, near-field; Kotiaho et al., 1996; Uetz and Roberts, 2002; Stratton, 2005; Rundus et al., 2010), in the degree of ornamentation (review of genus Schizocosa Stratton, 2005; Framenau and Hebets, 2007), and in the complexity of the visual display (Hebets and Uetz, 2000; Stratton, 2005). Various aspects of these courtship displays have been posited to enhance signal efficacy across signaling environments (Scheffer et al., 1996; Hebets and Uetz, 1999; 2000; Uetz et al., 2009), as signaling environments for spiders are exceptional in their complexity and variability (Elias and Mason, In Press).

The wolf spider *Rabidosa rabida* (Walckenaer) is particularly well suited to studies exploring the influence of the signaling environment on reproductive behavior. Male *R. rabida* perform complex courtship displays consisting of multiple components across different sensory modalities. The visual portion of *R. rabida* courtship involves palpal rotations and leg-waves, consisting of arches and extensions of darkly pigmented forelegs (Kaston, 1936; Rovner, 1968). Additionally, males produce a seismic component which is transmitted through the substrate via palpal stridulation (Rovner, 1967; 1975). The substrate for *R. rabida* consists of grassland plants, as they are found above the ground in the dense vegetation of open grasslands (Kuenzler, 1958). In addition to the heterogeneity of the seismic signaling substrate, individuals are reproductively active during both day and night (D. Wilgers pers. obs.; Rovner, 1967), introducing a highly variable visual signaling environment as well. Previous work on *R. rabida* has suggested that not only do both the visual and seismic courtship components play a role in conspecific interactions (Rovner, 1996), but that each signal modality is sufficient for female receptivity, potentially allowing males to maintain reproductive behavior at any time of day (Rovner, 1967; 1968). This previous work predominantly focused on female receptivity displays. Here, we look to extend this work by first assessing the potential information content, or condition-dependence, of components in these signaling modalities. We next examine male copulation success across signaling environments that vary in their transmission efficacies. Finally, we examine male courtship behavior across these same signaling environments to determine whether complex signaling facilitates plasticity in male courtship behavior.

2 Materials and Methods

2.1 Condition-dependence of signal components

We collected immature male spiders from Lancaster County, NE in 2007 (3–11 June) and 2008 (14 June). Individuals were housed in a climate controlled environment (24–27°C, 15:9 L:D cycle) in individual plastic containers (84 mm × 84 mm × 110 mm) with visual barriers. Individuals were immediately placed on an assigned diet treatment. As in previous wolf spider studies (e.g., Hebets et al., 2008b; Shamble et al., 2009; Rundus et al., In Press), we used diet manipulations to investigate the condition-dependence of components of visual and seismic signals. Briefly, upon collection, all males were randomly assigned to one of two diet treatments for the duration of the experiment: 1) high quantity diet (HD) – spiders were fed two body-size matched crickets *Acheta domestica*, twice per week, or 2) low quantity diet (LD) – spiders were fed two body-size matched crickets once every two weeks. All crickets were supplemented with fish flakes (TetraMin, Blacksburg, VA) and Fluker's cricket feed (Port Allen, LA).

Spiders were provided with water ad libitum. Individuals were checked for molts every 2–3 days to determine their time of maturation. To assess the efficacy of our diet manipulations, males were weighed within two days of their molt to maturation. After preservation, their cephalothorax width (mm) was measured 3 independent times using digital calipers, and averaged for analyses.

Foreleg Color Analysis We analyzed the foreleg coloration, a male secondary sexual trait that both appears and is fixed at maturation, of males raised on the different diet manipulations described above (2007: HD: n = 58, LD: n = 51; 2008: HD: n = 24, LD: n = 17). Additionally, we analyzed the foreleg coloration of males caught as adults in the field in 2008 (4 August; n = 27).

After sacrificing, male right forelegs were removed and frozen at -80° C. Prior to image capture, forelegs were allowed to thaw. Forelegs were placed on a clear microscope stage and illuminated from above using a 150-watt Lumina dual fiber optic light (Chiu Technical Corporation, Kings Park, NY, USA). The lateral side of each foreleg was photographed using a stereoscope (Leica MZ16, Bannockburn, IL, USA) and a Spot Flex digital camera (Model 15.2 64 MP, Diagnostic Instruments, Inc. Sterling Heights, MI, USA), under a 1.0 × objective and 1.2 × camera coupler. Images were imported onto a desktop computer using Image Pro Discovery v. 5.1 (MediaCybernetics, Inc., Silver Spring, MD). All foreleg images (diet manipulation and field caught) were captured on the same day, using the same settings and light levels, enabling direct comparisons among individuals.

Foreleg coloration was quantified using identical methods to previous studies working with foreleg color in wolf spiders (Shamble et al., 2009; Rundus et al., In Press). Briefly, images of each leg were imported into Adobe Photoshop CS2 and changed to grayscale. We analyzed the entire femur, patella, tibia, metatarsus, and tarsus of all forelegs and the tibia segment on leg II (for males in 2008) for mean segment image intensity (i.e. darkness, 'K' a numerical value where lower scores indicate darker images; 0= black → 255= white). Each measurement was taken once. Since foreleg coloration is highly correlated between all segments (Spearman's correlation, all $P < 0.001$), we calculated the mean image intensity across all foreleg segments for our analyses.

Sexually selected ornaments are expected to show a greater degree of condition dependence than similar non-sexually selected traits (Cotton et al., 2004), and thus we would expect to see greater degrees of difference in darkness between the diet treatments for leg segments that are presumably under sexual selection. To test this, we compared the tibia segments from the second pair of legs (non-ornamented) between males reared on the same diet manipulations in 2008. Analyses were performed in JMP v. 6 (SAS Institute Inc., Cary, NC, USA). Non-normal data were analyzed using non-parametric tests.

Seismic Analysis We analyzed the seismic component of male courtship displays for a subset of males raised on diet manipulations in 2007 (n = 15 / diet treatment). Male age ranged from 36-92 days ($\bar{x}$ =65.9), and there were no differences in age between diet treatments ($t_{28} = 0.51$, $P = 0.61$).

To remove the issue of pseudoreplication and to reduce any potential influence of individual female silk cues on male courtship behaviors, we provided males with multiple female cues simultaneously. Prior to each recording, 4 mature virgin female spiders were allowed to deposit silk on a piece of filter paper (Whatman #1 185 mm) for one hour each. Given the density of spiders at our collection location, males are highly likely to encounter silk cues from numerous females (D Wilgers, pers. obs.). Silk from mature females is known to elicit courtship in the absence of a female (Tietjen, 1979). The filter paper from which we recorded seismic signals was suspended 2.5 cm above the floor on a circular ring of acoustic foam with rubber footings. A 0.5 cm × 0.5 cm piece of retroreflective tape (3M Diamond Grade, 3M, Saint Paul, MN, USA) was placed in the center of the filter to increase the signal strength of the vibrometer. A transparent acetate wall was attached to a ring of high-density acoustic foam and placed on top of the filter paper to prevent the spiders from escaping. A female spider was placed on the outside of, and not in contact with, the recording arena – providing males with a visual stimulus only. While a female visual stimulus is not necessary to elicit male courtship, we added this component based on prior observations suggesting that males court longer with a visual stimulus of a female (D. Wilgers pers. obs.). A single female was present in a small confined space (5 cm diameter plastic vial), limiting their movements, outside of all test male arenas and thus, their presence is unlikely to explain any of our observed patterns.

Males were recorded in a soundproof chamber (50 cm × 37 cm × 43 cm) lined with loaded vinyl PSA and soundproof foam (Super Soundproofing Co., San Marcos, CA, USA) placed on a vibration isolation table (Minus K 50BM-8C, Minus K Technology, Inglewood,

CA, USA). Trials were illuminated in the enclosure with a Vita-lite full spectrum fluorescent bulb (Duro-Test Lighting Inc., Philadelphia, PA, USA) and filmed using a Logitech Webcam Pro 9000 (Logitech, Fremont, CA, USA). Seismic recordings were made using a laser vibrometer (Polytec PDV100), set for a peak velocity measurement range of ± 20 mm/s, with a low pass filter at 22 kHz, and at a 24 bit 48 kSa/s sample rate. Digital output from the vibrometer was recorded on an Apple iMac in Quicktime Pro, where it was synchronized with the video recordings. All vibration recordings were exported from Quicktime Pro as uncompressed AIFF files at 44.1 kHz sampling rate with 16-bit mono encoding.

At the beginning of trials, males were placed directly in the recording arena where we recorded up to five minutes of courtship (range 6–13 courtship bouts, $\bar{x}$ =10.3). The total number of courtship bouts recorded and analyzed for males in each diet treatment were similar (Mann-Whitney test, Z =0.95, P = 0.34). The seismic display of *R. rabida* consists of two components, a series of introductory bursts of pulses, followed by a distinct pulse-train, consisting of more rapid pulses increasing in frequency and amplitude until the end of the bout (Fig. 1; see description by Rovner, 1967). Using Raven Pro (v 1.3, Cornell Laboratory of Ornithology, Ithaca, NY), we blindly (with respect to diet treatment) analyzed all courtship bouts within a trial for the following parameters: 1) duration of introductory segment (sec), 2) pulse-train length (sec), 3) inter-bout interval (time between end of previous pulse-train and next introductory pulse; sec), 4) beginning pulse-train amplitude (dB, quantified as mean power over 100 ms), 5) maximum pulse-train amplitude (dB, quantified as mean power over 100 ms), 6) number of introductory pulse bursts, and 7) number of pulse bursts in pulse-train. Introductory segments and pulse-trains were both identified visually (from waveform) and by ear. The start of the introductory pulse segments were marked by the beginning of pulse bursts, while the beginning of pulse-trains were identified when pulse frequency and amplitude increased (Rovner, 1967). To control for differential attenuation of signal amplitude due to distance of the spider from the laser, we analyzed amplitude change by calculating the difference in beginning and maximum amplitudes within each separate pulse-train. We analyzed all courtship bouts performed in a trial and used the average (across all bouts) for each of the seismic display parameters in our statistical analysis. To test for differences in seismic display parameters based upon our diet treatments, we used a logistic regression with male diet as a response variable and the means of each parameter as predictor variables.

2.2 Reproductive success across signaling environments

We collected immature spiders (n = 194) from the same site in Lancaster County, NE in 2008 (9–12 July).

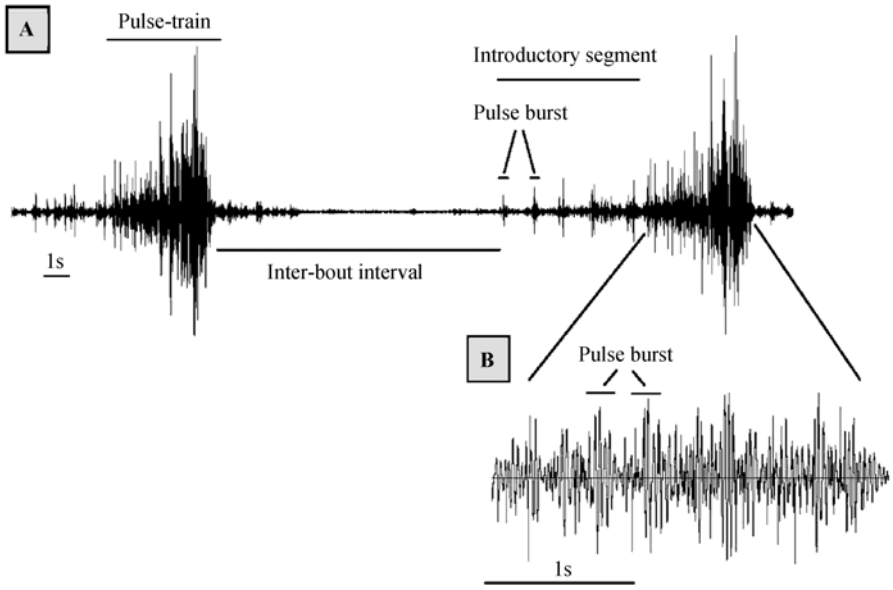

Fig. 1 Waveform of *R. rabida* seismic display showing (A) various parameters measured for influence of diet manipulation, and (B) magnified pulse-train showing discrete pulse bursts, consisting of individual pulses previously described as each individual waveform spike (Rovner, 1967)

The magnified portion does not represent the entire section indicated but is a shorter segment blown up for detail.

Spiders were brought back to the laboratory and housed in individual plastic containers (84 mm × 84 mm × 110 mm) with visual barriers. All individuals were housed in a climate controlled room at 27°C under a 15:9 Light:Dark cycle. Spiders were fed three body-size matched crickets *Acheta domestica*, once per week and provided water ad libitum. Crickets were supplemented with fish flakes (TetraMin, Blacksburg, VA) and Fluker's cricket feed (Port Allen, LA). We checked spiders 2–3 times per week for molts to determine the day of maturation.

We used a fully crossed 2 × 2 experimental design with respect to the signaling environment, in which we independently manipulated the visual (V) and seismic (S) environment by performing trials in the light (V+) versus dark (V-) and on filter paper (S+) versus granite substratum (S-). Thus, we performed single choice mating trials (1 female and 1 male) in 1 of 4 environments (V+/S+, V+/S-, V-/S+, V-/S-) that differed in their signal transmission. Light trials (V+) were performed under illumination from 2 full spectrum Vita-Lite 30-watt fluorescent bulbs (Duro-Test Lighting Inc., Philadelphia, PA, USA), while dark trials (V-) were performed in complete darkness with observations of the trial aided by infrared night vision goggles (Rigel 3200, Rigel Optics Inc., Washougal, WA, USA) and an infrared illuminator (Supercircuits IR20, Supercircuits, Austin, TX, USA). Spectral sensitivity data on wolf spiders, as well as the wandering spider, *Cupiennius salei*, provide no indication that these spiders can detect the IR wavelengths emitted by the illuminator (~ 850 nm; Devoe et al., 1969; Devoe, 1972; Barth, 2002). Seismic present trials (S+) were run using a filter paper substrate (Whatman #1 185 mm), while seismic absent trials (S-) were run using bottomless arenas placed on granite slabs, which like other types of rock are effective at ablating seismic signals of spiders (D. Wilgers, pers. observation; Elias et al., 2004). All trials were performed in circular plastic arenas (diameter = 20.2 cm, height = 7.3 cm) surrounded with white walls for visual barriers.

Females were 12–14 days post maturation when used in trials, the age at which females are most discriminating (Uetz and Norton 2007; D. Wilgers, unpublished data). Male age ranged from 11–20 days post maturation and was similar across signaling environments (Kruskal-Wallis, $\chi^2_3 = 1.39$, $P = 0.71$). All individuals were naïve virgins and used only once. Approximately 24 hrs prior to trials, males and females were given a small (~ 1/2 body size) cricket to standardize hunger levels and minimize the probability of pre-mating sexual cannibalism. All individuals were weighed (Ohaus Adventurer Pro AV64 Pine Brook, NJ, USA) just prior to their introduction to the arena; both female and male weights were similar across environments (Kruskal-Wallis tests, both $P > 0.31$). Females were placed in the mating arena at least 1 hr prior to their trial to acclimatize and deposit pheromone-laden silk. For introduction of the male, females were placed under a clear plastic vial. Males were allowed to acclimatize for ~ 1 min, and then the female's vial was lifted and the trial commenced. Trials lasted for 45 min, during which time we observed the following behaviors: latency to the first courtship, number of courtship bouts, male attempted mounts, female attacks, copulation, latency to copulation, cannibalism, and latency to cannibalism. After observing several trials, we noticed variability in the number of male courtship bouts that incorporated a leg-wave and began recording whether each courtship included a leg-wave. Since we did not begin recording this behavior at the beginning of the experiment, we have a reduced sample size for this variable.

To test the influence of the signaling environment on copulation success, we used a nominal logistic regression model with the presence/absence of both the visual and signaling environments as predictor variables for copulation success. All statistics were performed in JMP v. 6 (SAS Institute Inc., Cary, NC, USA). Non-normal data were analyzed using non-parametric tests. All results are reported as means ± 1 *SE*.

3 Results

3.1 Condition-dependence of signal components

At time of collection in both years, males were similar in mass (Table 1). Upon maturation, HD males were significantly larger (cephalothorax width) and in better body condition than LD males (mass (g)/cephalothorax width (mm); Table 1).

Foreleg coloration Male foreleg coloration was significantly influenced by diet quantity treatment, as HD males had overall darker forelegs than LD males (Mann-Whitney test, $Z = 8.5$, $P < 0.001$; Fig. 2a). Males placed on the same diet quantity manipulations in 2008 showed no differences in darkness of the tibia segments on the non-ornamented second leg (HD: $n = 24$, $\bar{x} = 106.3 \pm 1.9$; LD: $n = 15$, $\bar{x} = 111.7 \pm 3.5$; $t_{37} = 1.5$, $P = 0.15$). However, the overall darkness of the forelegs was again found to be significantly different (HD: $n = 20$, $\bar{x} = 40.2 \pm 1.0$; LD: $n = 14$, $\bar{x} = 69.9 \pm 2.6$;

Table 1 Effects of diet quantity manipulations on body measures of male *R. rabida*

		Male Diet Treatment (*n*)		
Year	Body Measure	LD	HD	*P*-Value[a]
2007	Initial Mass (mg)	110.1 ± 8.0 (51)	113.4 ± 7.0 (58)	0.78
	CW (mm)	4.31 ± 0.06 (48)	4.87 ± 0.06 (53)	< ***0.001***
	Condition[b]	43.6 ± 1.2 (48)	54.1 ± 1.2 (53)	< ***0.001***
2008	Initial Mass (mg)	42.3 ± 1.7 (17)	47.6 ± 2.6 (24)	0.43
	CW (mm)	3.18 ± 0.05 (16)	4.27 ± 0.07 (24)	< ***0.001***
	Condition[b]	23.4 ± 0.6 (16)	42.6 ± 1.3 (24)	< ***0.001***

Means ± SE shown for each parameter

[a]P-values reported from Mann-Whitney tests on differences between diet treatments.

[b]Condition calculated as ratio of body mass at maturation (mg) / cephalothorax width (mm).

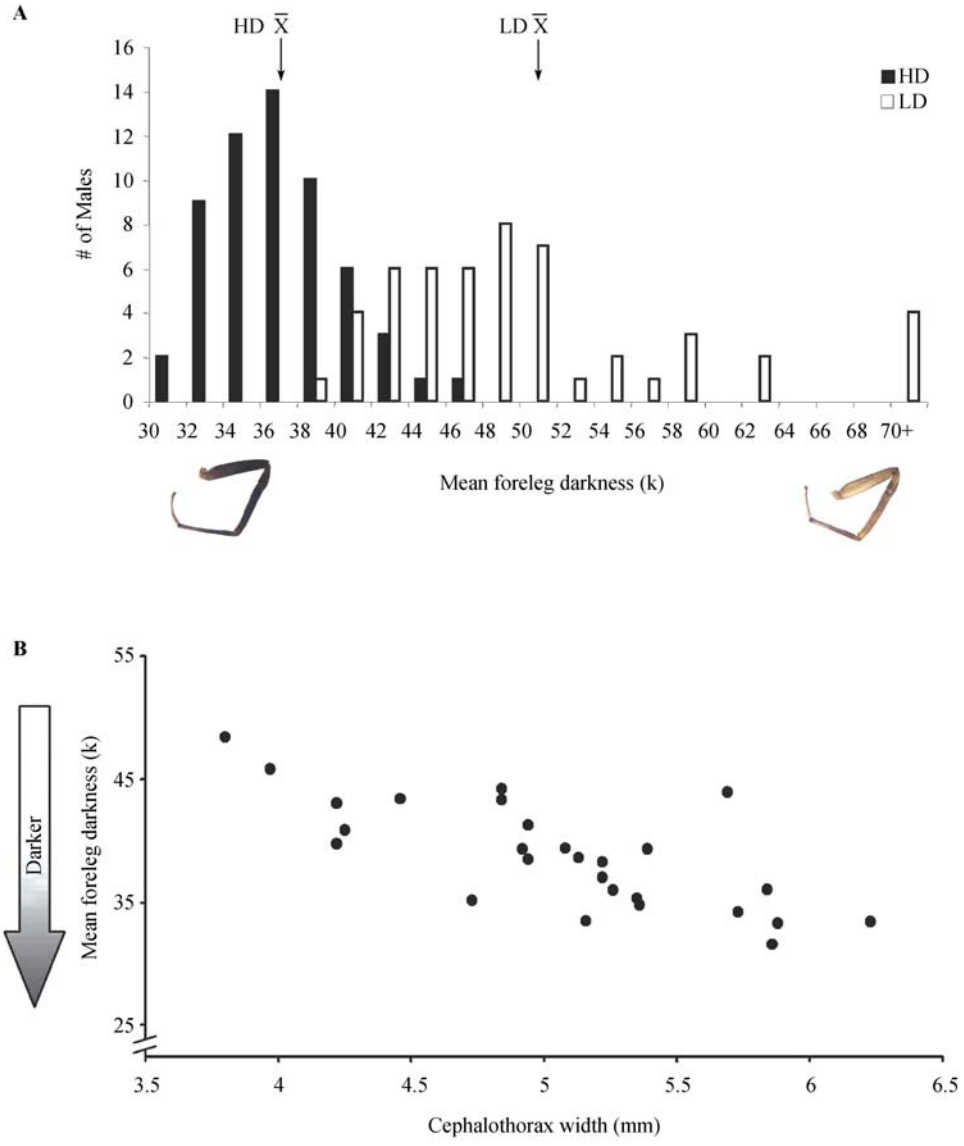

Fig. 2 Variability in *R. rabida* foreleg coloration

A. Across males varying in juvenile diet via diet-quantity manipulations (HD: $n = 58$; LD: $n = 51$). Arrows below $\bar{x}$ denote means for HD and LD males. Lower 'K' values indicate darker legs. Foreleg pictures under x-axis provide an example of the extremes witnessed in foreleg darkness. **B**. Across mature males caught in the field varying naturally in size ($n = 27$; Spearman's correlation, $\rho = -0.74$, $P < 0.001$).

Mann-Whitney test, $Z = 4.9$, $P < 0.001$). Measurements from mature males caught from the field revealed a significant negative correlation between body size and foreleg darkness (Spearman's correlation, $\rho = -0.74$ $P < 0.001$; Fig. 2b), identical to the pattern observed in our diet manipulations.

Seismic component Seismic display parameters within each bout significantly varied with diet (Overall Model: $\chi^2_5 = 21.2$, $P < 0.001$; Table 2). The length of time spent exhibiting each of the major seismic components differed between diet groups - LD males had longer introductory segment durations than HD males, while HD males produced longer pulse-trains (Fig. 1, Table 2). We found no differences between diet treatments in other display variables, such as number of pulse bursts per second in either the introductory segment or pulse-train, or the relative increase in amplitude within each pulse-train bout (Table 2). Males spent equal amounts of time signaling, as the overall length of each seismic bout and the time between bouts did not differ between HD and LD males (bout length: $t_{28} = 0.87$, $P = 0.39$; inter-bout interval: Mann-Whitney test, $Z = 0.75$, $P = 0.46$).

3.2 Reproductive success across signaling environments

A total of 97 male-female pairs were run in the variable signaling environments. Copulations occurred in 27% of trials, while the probability of cannibalism during trials was 13%, but was equally distributed across treatments (Likelihood Ratio, $\chi^2_3 = 0.2$, $P = 0.98$). In five trials cannibalism occurred before males began courtship. For those trials in which males courted ($n = 92$), mating frequency was highly dependent on the signaling environment (Overall Model: $\chi^2_3 = 22.9$, $P < 0.001$; Fig. 3). Copulation frequencies were influenced by the presence/absence of both the visual and seismic signals, however there was no interaction between the two (visual: $\chi^2_1 = 3.97$, $P = 0.046$; seismic: $\chi^2_1 = 21.98$, $P < 0.001$; visual X seismic: $\chi^2_1 = 2.02$, $P = 0.16$). While copulation success was significantly reduced when either modality was removed, the presence/absence of the seismic signal had a greater relative impact on copulation frequencies compared to the visual environment (Fig. 3), as copulation frequencies in seismic-only trials (V-/S+) were significantly greater than visual-only trials (V+/S-; Likelihood ratio, $\chi^2_1 = 5.31$, $P = 0.02$). Copulation frequencies in trials with both modalities present (V+/S+) were significantly greater than in trials with only visual (V+/S-: Likelihood ratio, $\chi^2_1 = 9.72$, $P = 0.002$), but not when compared to seismic only (V-/S+; Likelihood ratio, $\chi^2_1 = 0.73$, $P = 0.39$). No copulations occurred when both signal modalities were removed (V-/S-), which was significantly less than trials with only the seismic modality present (Likelihood ratio, $\chi^2_1 = 12.46$, $P < 0.001$), but not statistically less than trials with only the visual modality present (Likelihood ratio, $\chi^2_1 = 3.27$, $P = 0.07$).

Across treatments, male motivation to mate appeared similar. The latency to a male's first courtship (Kruskal-Wallis, $\chi^2_3 = 3.55$, $P = 0.31$) and attempted mounts of the female (Kruskal-Wallis, $\chi^2_3 = 2.57$, $P = 0.46$) did not differ across treatments. However, male courtship rate (# courtship bouts / sec) was dependent on the signaling environment (Kruskal-Wallis, $\chi^2_3 = 17.27$, $P < 0.001$; Fig. 4a). Post-hoc pairwise comparisons using Mann-Whitney tests ($P < 0.05$) revealed that males courted at higher rates in the V+/S+ trials than either of the dark treatments, and males courted at higher rates in all signaling environments compared to trials run in the absence of both modalities (Figure 4a). However, despite these differences in courtship effort, males gained copulations just as fast regardless of the signaling environment, as the time from first courtship to copulation did not differ (Kruskal-Wallis, $\chi^2_2 = 1.56$, $P = 0.46$).

Table 2 Variability in seismic display parameters between high and low quantitiy diet males of *R. rabida*

Signal Parameter	HD (n=15)	LD (n=15)	Chi-Square[a]	P-value
Introductory Segment Duration (sec)	4.30 ± 0.23	5.24 ± 0.47	13.4	< 0.001
Pulse-train Duration (sec)	3.57 ± 0.15	3.20 ± 0.12	11.9	< 0.001
Introductory Pulse Bursts / Sec	2.06 ± 0.10	2.14 ± 0.13	0.01	0.91
Pulse-train Pulse Bursts / Sec	4.56 ± 0.24	4.41 ± 0.12	2.99	0.08
Pulse-train Amplitude Increase (dB)	12.22 ± 0.51	10.52 ± 0.60	2.16	0.14

Means ± SE shown for each parameter.

[a] Chi-Square values from a logistic regression model incorporating all signal parameters to predict male diet treatment(Overall Logistic Regression Model: $P < 0.001$).

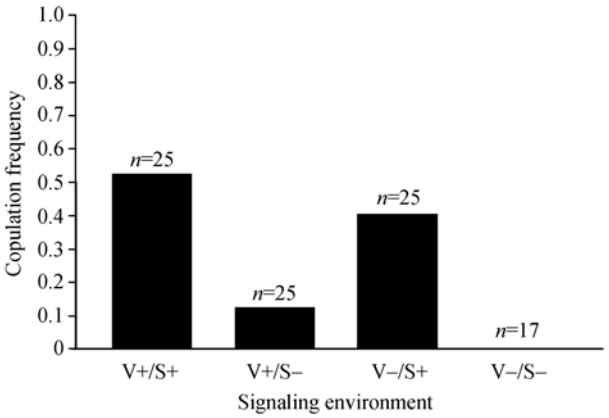

Fig. 3 Influence of signaling environment on copulation frequencies in *R. rabida*

Male-female pairs were placed in mating trials in the presence (+) or absence (-) of the visual (V) or seismic (S) signal.

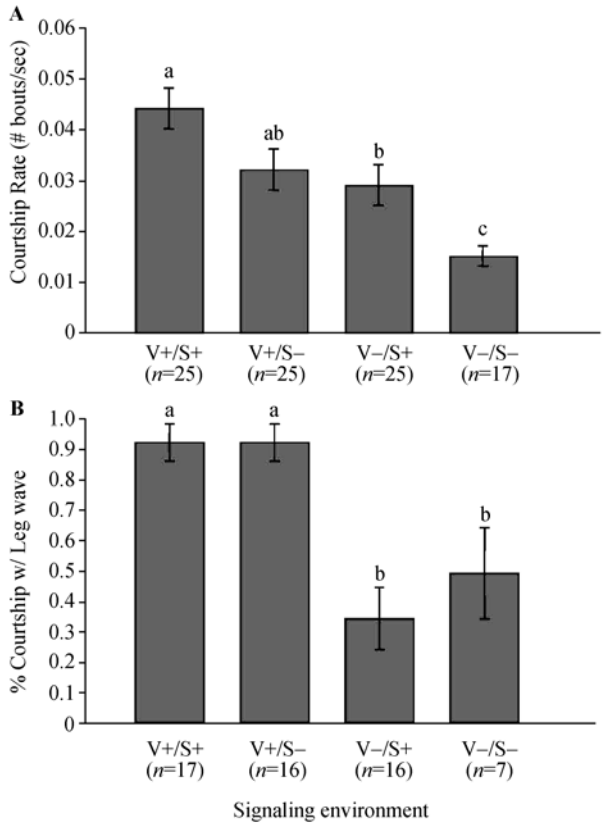

Fig. 4 Influence of the signaling environment on *R. rabida* male (A) courtship rate and (B) display composition

Male-female pairs were placed in mating trials in the presence (+) or absence (-) of the visual (V) or seismic (S) signal. Letters denote significant differences detected by post-hoc pairwise comparisons using Mann-Whitney tests, $P < 0.05$.

Interestingly, we found that males altered the composition of their complex display depending on the signaling environment (Kruskal-Wallis, $\chi^2_3 = 26.95$, $P < 0.001$; Fig. 4b). Males significantly decreased the proportion of courtship bouts that incorporated a leg-wave in treatments run in complete darkness (V-/S+ and V-/S-), while the presence/absence of the seismic modality had no influence on the number of leg-waves incorporated into courtship displays (Fig. 4B; post-hoc pairwise comparisons using Mann-Whitney tests, $P < 0.05$).

3 Discussion

The multimodal courtship display of male *Rabidosa rabida* is well suited for communication in signaling environments that vary in modality-specific transmission. Both foreleg ornamentation and the seismic display are condition-dependent, and reflect past foraging history. As such, these signals have the potential to convey similar information, and potentially act as redundant components or signals (Møller and Pomiankowski, 1993). Additionally, visual and seismic signals in isolation are each sufficient to maintain male reproductive success, supporting a back-up function of complex signaling, where each component backs up the other in the face of environmental variability (Candolin, 2003; Hebets and Papaj, 2005). The potential redundancy of information and sufficiency of each signal modality for mating would make it possible for males to maintain reproductive success irrespective of variation in the signaling environment. Furthermore, our results highlight an additional advantage to complex signaling – flexibility in the composition of courtship displays – which could enable males to adjust the composite make-up of courtship displays depending upon current signaling conditions. Together, our results are consistent with the hypothesis that the signaling environment of *R. rabida* has played a major role in the evolution of their complex courtship display.

In *R. rabida* courtship displays, we found display components of each modality, the visual foreleg coloration and the seismic courtship signal, to be condition-dependent. Similar condition-dependent display components have been found across several lycosids (e.g., Kotiaho, 2000; Uetz et al., 2002; Gibson and Uetz, 2008; Hebets et al., 2008b; Shamble et al., 2009; Rundus et al., In Press). With respect to the seismic courtship signal specifically, our results show that males vary in the structure of their seismic display depending upon their condition. HD males produced longer pulse-trains while LD males had longer introductory segments. Our observed differences in amplitude and frequency of pulses between the introductory and pulse-train components suggest that the pulse-train is

likely more costly to produce. One possibility is that only males in good condition can afford this lengthy display; and that poor condition males may instead invest more time in a less costly signal component (e.g., introductory segment). Although both quantified displays components (foreleg coloration and seismic signal) were shown to be condition-dependent, our diet manipulations involved a sustained diet treatment that included both juvenile and adult life stages. It remains possible, therefore, that juvenile versus adult foraging efficacy influence visual and seismic components differently, leaving the possibility that different signal components convey different information (i.e., multiple messages; Møller and Pomiankowski, 1993). Additionally, numerous other display components exist in *R. rabida* courtship (e.g., pedipalpal color and movement and foreleg movement) that were not measured in this study. Future work focusing on both receiver responses to isolated display components, as well as the incorporation of additional display components, are essential to fully understand complex signal function in this species.

In *R. rabida*, we found that copulation success is maintained with only one modality present, and that both visual and seismic signals play a role in *R. rabida* mating success, corroborating previous studies on this species (Rovner, 1967; 1968; 1996). While we found the seismic signal to be relatively more important in female mate choice decisions, a result that has been found across multiple species of *Schizocosa* wolf spiders (Scheffer et al., 1996; Hebets and Uetz, 1999; Hebets, 2005; 2008; Rundus et al., In Press; but see Rundus et al., 2010), copulation success was maintained, albeit at lower levels, with just the visual signal present. The maintenance of reproductive success regardless of signal transmission suggests environmental variability could have selected for complex signal components in *R. rabida* to function as efficacy backups.

Interestingly, we found that male *R. rabida* courtship rate and display composition is flexible and responsive to the signaling environment. Males tended to court females at the highest rates in environments where both modalities were transmitted. Males also reduced the incorporation of one visual component, the foreleg wave, when courting in an environment that does not transmit visual signals. Dynamic courtship signaling via the alteration of display rates, intensity, or signaling location have been found in response to receivers (e.g., Patricelli et al., 2002; Dukas, 2008) as well as to the signaling environment (e.g., Reynolds, 1993; Brumm, 2004; Ord et al., 2007). However, fewer studies have demonstrated that signalers will alter display type or composition based upon the signaling environment (e.g., Jackson, 1992; Taylor and Jackson, 1999; Taylor et al., 2005; Grafe and Wanger, 2007; Peters et al., 2007). Dynamic flexibility in displays in response to environmental variability has been shown to be adaptive by maintaining signal detectability (Ord et al., 2010). In addition, given the variety of costs associated with signaling (e.g., metabolic, predation; Andersson, 1994; Bradbury and Vehrencamp, 1998), flexibility in complex signal composition in response to each context (e.g., environment, predator proximity) could limit costs by reducing production of unnecessary or costly components while continuing production of others and maintaining (at some level) the associated benefits. In *R. rabida*, the production of the foreleg wave may be costly, as we have evidence that LD males incorporate significantly fewer foreleg waves in their displays (Wilgers unpub. data). Alternatively, visual feedback from females may be important in eliciting the full production of *R. rabida* complex displays. Consistent with this alternative, previous studies suggest that male *R. rabida* reduce activity and remain stationary under reduced illumination (Frings, 1941; Rovner, 1991), indicating detection of females in proximity as a possible release mechanism resulting in the greater occurrences of full courtship displays. Female visual feedback has also been previously found to influence inter-courtship intervals and the brevity of the male visual displays in *R. rabida* (Rovner, 1967; 1968), which could also help to explain the observed increased courtship rates of males in the light. These explanations are not mutually exclusive and all may play a role in the flexible composition of courtship displays we witnessed across signaling environments in *R. rabida*.

In nature, given the complex signaling environment of *R. rabida*, females may frequently find themselves the recipients of courtship signals via only one sensory modality. Here we provide evidence that both the visual signal and the seismic signal can potentially convey redundant information regarding a male's condition, and that both of these modalities are important during mate choice decisions in *R. rabida*. Our results suggest that these signals may act as both content and efficacy backup signals, which seems adaptive given the natural history of *R. rabida*. Additionally, when faced with environmental variability in the efficacy of modality-specific signal transmission, multimodal signals may afford males the flexibility to reduce costs associated with the production of ineffective signals by removing

them from their repertoire and relying upon signals for which transmission remains effective. Large-scale comparisons of environmental and corresponding signal complexities across taxa may shed light on the role of signaling environment on the evolution of signal complexity.

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